Deep-Sea Gastropods of the Genus *Aforia* (Turridae) of the Pacific: Species Composition, Systematics, and Functional Morphology of the Digestive System

by

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Abstract. The composition and distribution of deep-sea species of the genus *Aforia* from the Pacific are studied. Three new subgenera, **Dallaforia**, **Abyssaforia** and **Palaeoaforia**, are described. *Steiraxis* is considered as a taxon of the subgeneric level within *Aforia*. Three new species (*Aforia abyssalis*, *A. moskalevi* and *A. kupriyanovi*) and one new subspecies (*A. aulaca alaskana*) are described.

The anatomies of seven species of *Aforia*, including the type species, are presented. On the whole, the structure of all main organ systems is similar in most of the species. None of the species has an invaginable part of the rhynchodaeum. It is shown that Toxoglossa possess an intraembolic proboscis characterized by a buccal mass situated near its base.

An explanation is proposed of the feeding mechanism in turrids having a well-developed subradular membrane and "nontoxoglossate" radular teeth. The explanation is based on findings of marginal teeth held by a sphincter of the tip of the proboscis of *Aforia* species. Thus, marginal teeth perform a double function, being used both in the buccal cavity and at the tip of the proboscis as in the higher Toxoglossa.

An analysis of the geographical distribution and history of members of *Aforia* shows that the main factor conditioning the evolution of the genus is its adaptation to low water temperatures.

INTRODUCTION

Gastropods of the genus *Aforia* are among the largest (adult shell sizes up to 92 mm) and most widely distributed members of the family Turridae in the Pacific. Species of *Aforia* are mostly found in relatively deep waters, and descriptions of the specific composition of *Aforia* in bathyal and abyssal faunas are fragmentary. There are very few data on the distribution of species, while data on anatomy are almost absent.

Several rare and undescribed species of *Aforia* have been found recently by Soviet deep-sea expeditions. Our investigations of the morphology of their shells, radulae, and soft parts have allowed us (1) to revise, to some extent, the generic composition and to erect infrageneric taxa, (2) to specify the identity and distribution of bathyal and abyssal species (of which three species and one subspecies appear to be new), and (3) to analyze the functional morphology of the digestive system of the species studied.

For the comparative analysis of *Aforia* morphology, an investigation was carried out of the anatomy of the genus type species, *A. circinata* (Dall), which is not a true deep-sea species.

All type specimens of described species are deposited in the Zoological Museum of Moscow State University. Registration numbers are indicated in the descriptions of species.

MATERIALS AND METHODS

Materials for the study were collected by Soviet expeditions on the research vessels *Vityaz, Dmitry Mendeleev, Akademik Kurchatov,* and *Gidrobiolog.* Coordinates of stations where mollusks were collected are listed in the descriptions of species.

The morphology of the digestive system was studied histologically. The anterior part of the system (including the proboscis with rhynchodaeum, poison gland, and a part of the oesophagus) or the molluscan body after removing the visceral mass and mantle were dehydrated and embedded in paraffin; sections 8–10 μm thick were cut. Sections were stained with haematoxylin-eosin and Mallory's stain. Semidiagrammatic representations of the anterior part of the digestive system were made. Poison and salivary glands, together with the radular sac, were represented stereoscopically, but the nerve ring was not figured. In studies of the odontophore of *Aforia circinata,* part of the buccal mass with radular sac was sectioned transversally.

Examinations of the mantle complex of organs and the penis were carried out with a stereomicroscope at magnifications of 16–32 times. Radulae for light microscopy were removed together with the radular sac and placed into a sodium hypochlorite solution to dissolve the tissues, with subsequent transfer to distilled water, cleaning, and embedding in glycerol. Radular teeth of two species were also prepared for scanning electron microscopy. After dehydration in alcohol and acetone, the teeth were mounted on sticky tape, coated with gold, and examined with a JSM-50A scanning electron microscope.

GENERAL ANATOMY OF
EXAMINED SPECIES

The body of deep-sea species of *Aforia* lacks pigmentation. The head is well distinguished from the body; eyes are absent. The morphology of the mantle complex is similar in all species. The osphradium and gill are large, the hypobranchial gland is moderately developed, and an anal gland is absent. All species examined have an accessory pedal gland situated in the depression in the middle part of the marginal glandular cleft. The epithelial lining of the accessory gland is similar to the rest of the marginal cleft. The most probable function of the gland is lubrication of the foot.

Close attention was paid to the anterior part of the digestive system, as its morphology is the most variable among Turridae. The generalized scheme of organs of the body haemocoel of *Aforia* is represented in Figure 4A.

The species have a more or less long proboscis situated in the rhynchocoel (rhynchodaeal cavity or proboscis sheath). The proboscis can be stretched out through the rhynchostome, which is surrounded with a very large, powerful sphincter. The buccal mass lies at the base of the proboscis. The buccal tube leads from the buccal cavity to the mouth at the tip of the proboscis. The radular sac opens into the buccal cavity. Near the entrance of the radular sac two ducts of salivary glands open. Large salivary glands, which may unite to form a single large one, are placed near or above a large nerve ring (not figured). A long poison gland opens ventrally behind the buccal mass. The poison gland has a large and powerful distal muscular bulb that functions as a propulsive organ.

SYSTEMATIC DESCRIPTIONS

Class Gastropoda

Subclass Pectinibranchia Blainville, 1814

Order Toxoglossa Gray, 1853

Family Turridae Swainson, 1840

Subfamily Turriculinae Powell, 1942[1]

Genus *Aforia* Dall, 1889

Type species: *Pleurotoma circinata* Dall, 1873 (O.D.).

The mollusks under consideration have been described in such genera as *Pleurotoma, Leucosyrinx, Aforia, Irenosyrinx,* or *Steiraxis.* However, in recent works only the latter three names are used.

The genus *Irenosyrinx,* with type species *Pleurotoma (Leucosyrinx) goodei* Dall, 1890, was described by DALL (1908) for species close to those of *Aforia* but differing (at least as type species) by the structure of the operculum. In adult specimens of *I. goodei* the operculum has a subcentral nucleus and looks like that of *Buccinum* whereas the *Aforia* representatives have an elongate operculum with a terminal nucleus. Subsequently, however, authors considered these differences insignificant (GRANT & GALE, 1931; POWELL, 1942, 1966, 1969; MCLEAN, 1971). We agree with this subsequent opinion because the considered group of species is rather homogenous and the species have similar morphologies of the shell, radular teeth and soft body, while the operculum with subcentral nucleus is known only for *A. goodei.* Such opercular morphology of the specimen studied by Dall can probably be considered an abnormal individual aberration caused by damage during growth, which also occurs sometimes in other turrids. This point of view is supported further by the fact that opercula of younger specimens also investigated by DALL (1908) have terminal nuclei similar to those of other species of *Aforia.* The division of *Aforia* and *Irenosyrinx* proposed by BOUCHET & WAREN (1980), based only on the fact that the type species of *Aforia* is a shallow-water boreal north Pacific species whereas that of *Irenosyrinx* is an abyssal eastern Pacific species, is considered groundless.

The monotypic genus *Steiraxis* was established by DALL

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[1] POWELL (1969) and CERNOHORSKY (1972) considered that the name Turriculinae Powell, 1942, cannot be used, being a junior homonym and, therefore, the available name for this taxon would be Cochlespirinae Powell, 1942. Recently, some authors have accepted this statement. However, according to the *International Code of Zoological Nomenclature,* the names Turriculinae Carpenter, 1861, and Turriculinae A. Adams, 1846, based on *Turricula* Fabricius, 1823 (Mitridae) (non *Turricula* Schumacher, 1817 [Turridae]) are not senior homonyms of Turriculinae Powell, 1942 (Article 54[1]), since the former two names are invalid (Article 39) and unavailable (Article 11[e]). Therefore, Turriculinae Powell, 1942, should be considered as an available and valid name.

(1896), with type species *Pleurotoma (Steiraxis) aulaca* Dall, 1896. According to Dall and all later authors, the principal feature separating this genus from *Irenosyrinx* (=*Aforia*) is stronger spiral sculpture equally developed on the whole surface of the shell whorls. However, the presence of the below-described abyssal species *A. abyssalis* sp. nov., which has sculpture intermediate between typical *Aforia* and *Steiraxis,* forces us to place *S. aulaca* in the genus *Aforia* while the name *Steiraxis* can be used for a subgenus within *Aforia.*

Peculiarities of the shell and radular tooth morphology and bathymetric distribution of the species of *Aforia* allow us to divide the genus into five subgenera. The diagnostic features of the subgenera are summarized in Table 1.

Subgenus *Aforia s.s.*

The shell spiral sculpture is represented by narrow, low ribs, being very slight on the shoulder. A weakly to moderately pronounced spiral keel is usually situated on the lower part of the shoulder. Marginal teeth of the radula are very small, and the shell height–tooth length ratio exceeds 100 (up to 180).

Species of the subgenus inhabit sublittoral and bathyal waters of the Pacific, the southwestern Atlantic, and the southeastern part of the Indian Ocean.

From our point of view the following nominal species should be included in the nominal subgenus: *Aforia circinata* (Dall, 1873), *A. insignis* (Jeffreys, 1883), *A. magnifica* (Strebel, 1908), *A. lepta* (Watson, 1881), *A. staminea* (Watson, 1881), *A. gonioides* (Watson, 1881), *A. goodei* (Dall, 1890), *A. persimilis* (Dall, 1890), *A. persimilis leonis* (Dall, 1908), *A. persimilis blanca* (Dall, 1919), *A. amycus* (Dall, 1919), *A. kinkaidi* (Dall, 1919), *A. hondoana* (Dall, 1925), *A. okhotskensis* Bartsch, 1945, *A. chosenensis* Bartsch, 1945, *A. sakhalinensis* Bartsch, 1945, *A. diomedea* Bartsch, 1945, *A. japonica* Bartsch, 1945, and *A. moskalevi* Sysoev & Kantor, sp. nov.

The above list includes names that have been only proposed, but at present we cannot estimate the validity of many of them because, on the one hand, we have too little material and, on the other hand, a detailed study on the shallow-water species systematics was beyond the scope of our work. It should be noted that, according to many authors, most if not all of the names proposed by BARTSCH (1945) should be synonymized with *A. circinata* (see POWELL, 1969) and all bathyal eastern Pacific species should be considered as a single species, *A. goodei* (see MCLEAN, 1971).

Aforia (Aforia) circinata (Dall, 1873)

(Figures 3A, C–E, 4B, C, 7A–D)

Material: Our specimens were collected near Iturup Island (Kurile Islands) at a depth of about 100 m (R/V *Gidrobiolog*).

Digestive system (Figure 7): The proboscis is long; in studied specimens it was stretched out through the rhynchostome. The buccal mass is large and pyriform, with a deep fold at the upper part. The walls of the buccal mass are thick, becoming thinner in the anterior part. The buccal tube is of a small diameter without folds along the buccal mass. The rhynchodaeum is strongly folded. The buccal tube forms a small expansion with a sphincter near the proboscis tip. The salivary glands are united as one large gland located above the oesophagus. Paired salivary ducts open into the radular sac near its entrance to the buccal cavity. The epithelium of the buccal cavity forms high folds, the largest of which are at the bottom of the cavity near the entrance of the radular sac (Figure 7B). The odontophore is of medium size with four subradular cartilages (Figure 7D) united in two pairs and connected by a muscular symphysis in the anterior part of the odontophore (Figure 7C). The radular sac is surrounded with a thick layer of muscles and is lined inside with a thick cuticular layer. The poison gland is large, with a greatly decreased diameter near its opening into the oesophagus. The muscular bulb is of medium size and oval. The oesophagus sharply increases in diameter posterior to the nerve ring. The stomach typically has a U-shape form and receives two ducts of the digestive gland. The radula is of typical form for the genus (Figures 3C–E). The central teeth are weak and thin. The marginal teeth are small. The shell height–tooth length ratio is 180.0.

Aforia (Aforia) lepta (Watson, 1881)

(Figures 1F, G, 5B, 6E–H, 8A–E)

Pleurotoma (Surcula) lepta WATSON, 1881:391, 1886:288, pl. XVIII, fig. 7.

Material: R/V *Dmitry Mendeleev*, station 1276, 48°25′S, 171°42′E (SE of New Zealand), depth 1100–1200 m, trawl Sigsbee, 1 specimen.

Shell: The shell of our specimen is very similar to that described by Watson (1886), differing in its smaller size (the shell height is 14.1 mm), less numerous whorls, and less well-developed spiral keel, especially on the penultimate whorl; spiral sculpture is more uniform, and intercalate threads between primary ones are absent.

The protoconch sculpture and also the operculum, radula and soft-body morphology, which were not studied previously, are described here. The operculum is small and drop-shaped (Figure 5B). The protoconch consists of 1.5 rapidly increasing whorls sculptured with very weak, thin, and inconspicuous spiral folds.

Anatomy (Figures 6E–H): The mantle is thin and the osphradium and gill are clearly seen through it. The siphon is short and contracts strongly during fixation. The propodium of the foot is narrow with a deep cleft; the accessory pedal gland is weak. The head is well distinguished from the body; the tentacles are short and rounded at the tip.

Table 1

Characters of the subgenera of *Aforia*.

Subgenus	Spiral ribs	Spiral keel	Shell height–tooth length ratio
Aforia s.s.	narrow, low, very slight on the shoulder	present, variously developed	107–180
Steiraxis	very strong, equally developed throughout the shell surface	present, strong	about 70
Abyssaforia	narrow, prominent, equally developed throughout the shell surface	none	57–90
Dallaforia	strongly inequal on the shoulder and on the rest of the whorl	none	about 100
Palaeoaforia	narrow, weak, smoothed on the shoulder	present, double	—

The rhynchostome has well-developed lips; its sphincter is very large.

Mantle complex (Figure 6G): The osphradium and gill are very large. The gill lamellae are tall and triangular; their height is nearly equal to the base width. At the inner side of the lamella a thickened cuticulized flagellum is situated. The flagellum adheres to the lamella. The gill extends nearly to the mantle outer edge but its lamellae are low there. The osphradium is flattened. The hypobranchial gland is poorly developed and is covered with a thick gel-like mucosal layer. The pallial oviduct is of small diameter and the female gonopore opens on a small rounded eminence. The rectum has a very small diameter. It lies along the surface of the oviduct; the anus opens nearer to the outer edge of the mantle than the gonopore does. There is a short and narrow transverse fold in the right part of the mantle.

Digestive system (Figure 8): The proboscis is small; its epithelium is formed by very tall gobletlike cells (Figure 8B). The buccal mass is of medium size with relatively thin walls. The buccal tube forms a fold along the buccal mass. In the anterior part, the buccal tube forms a small sphincter. Retractor muscles of the proboscis pass along its lumen and attach near the tip. The rhynchodaeum is folded and covered with a thick cuticular layer. The paired salivary glands are large, and their ducts are of small diameter, slightly coiling. The muscular bulb of the poison gland is small. Odontophore cartilages are absent, being replaced by a strong muscular fold. The oesophagus grad-

ually widens posterior to the entrance of the poison gland. The stomach is typically U-shaped, containing two ducts of the digestive gland. The central radular teeth are very thin (Figure 8D). The marginal teeth are small (Figures 8D, E). The shell height–tooth length ratio is 100.7.

Distribution: The species was previously known from two localities—the Australian-Antarctic Rise (R/V *Challenger,* station 157, 53°55′S, 108°35′E, type locality) and near Kerguelen Island (WATSON, 1886; CANTERA & ARNAUD, 1984). Our specimen was found in the New Zealand underwater plateau and, therefore, the species range is greatly extended eastward. The species lives at depths of 360 to 3560 m.

Aforia (Aforia) **moskalevi**
Sysoev & Kantor, sp. nov.

(Figures 1E, H, 5A, 6A–D, 9A–G)

Material: R/V *Dmitry Mendeleev,* station 1314, 59°58′S, 158°07′E (SW Pacific), depth 3010–3030 m, trawl Sigsbee, 2 specimens—holotype (No. LC 5360) and paratype (No. LC 5361).

Description of holotype: The fusiform shell is thin and consists of 4.5 preserved whorls. The protoconch is lost, as the first preserved whorl is eroded. Whorls are slightly convex and angulate at the periphery. The whorl shoulder is flattened and sloping. There is a very weak spiral fold on the shoulder of the body whorl. Axial sculpture is represented only by numerous thin growth lines, some of them being rather more pronounced, especially below the shoulder. Spiral sculpture of the upper part of the whorl consists of threadlike, weak, flattened ribs irregularly displaced and separated by interspaces twice as wide. On the lower part of the whorl, spiral ribs are larger, narrow, rounded, irregularly disposed, and separated by interspaces that are 2–4 times wider than rib widths. In some interspaces, there are much weaker secondary ribs. As the spiral ribs cross the strongest growth lines, they form reticulate sculpture. The aperture is wide and oval. The outer lip is broken. The inner lip is smoothly curved, coated with thin callus. The siphonal canal is long, slightly curved. The sinus, judging by growth lines, is deep, wide, and rounded; its apex is situated some distance above the middle of the whorl shoulder. The shell color is gray. The shell height is 33.4 mm, the height of the body whorl is 25.5 mm, the aperture height is 20.8 mm, and the shell diameter is 12.2 mm.

The paratype is smaller (the shell height is 27.2 mm) and poorly preserved. Its shell is quite similar to the holotype. We have studied the anatomy of the paratype.

The operculum is small and roundly triangular, with a terminal nucleus (Figure 5A).

Anatomy (Figures 6A–D): The mantle is thick, and the osphradium and gill are seldom seen through it. The mantle edge is uneven; it has a distinct notch corresponding to

Figure 1

A and B, *Aforia crebristriata* (Dall), R/V *Vityaz,* stat. 4173, shell height of 40.4 mm. C and D, *A. **kupriyanovi*** sp. nov., holotype. E and H, *A. **moskalevi*** sp. nov., holotype. F and G, *A. lepta* (Watson), R/V *Dmitry Mendeleev,* stat. 1276, shell height of 14.1 mm.
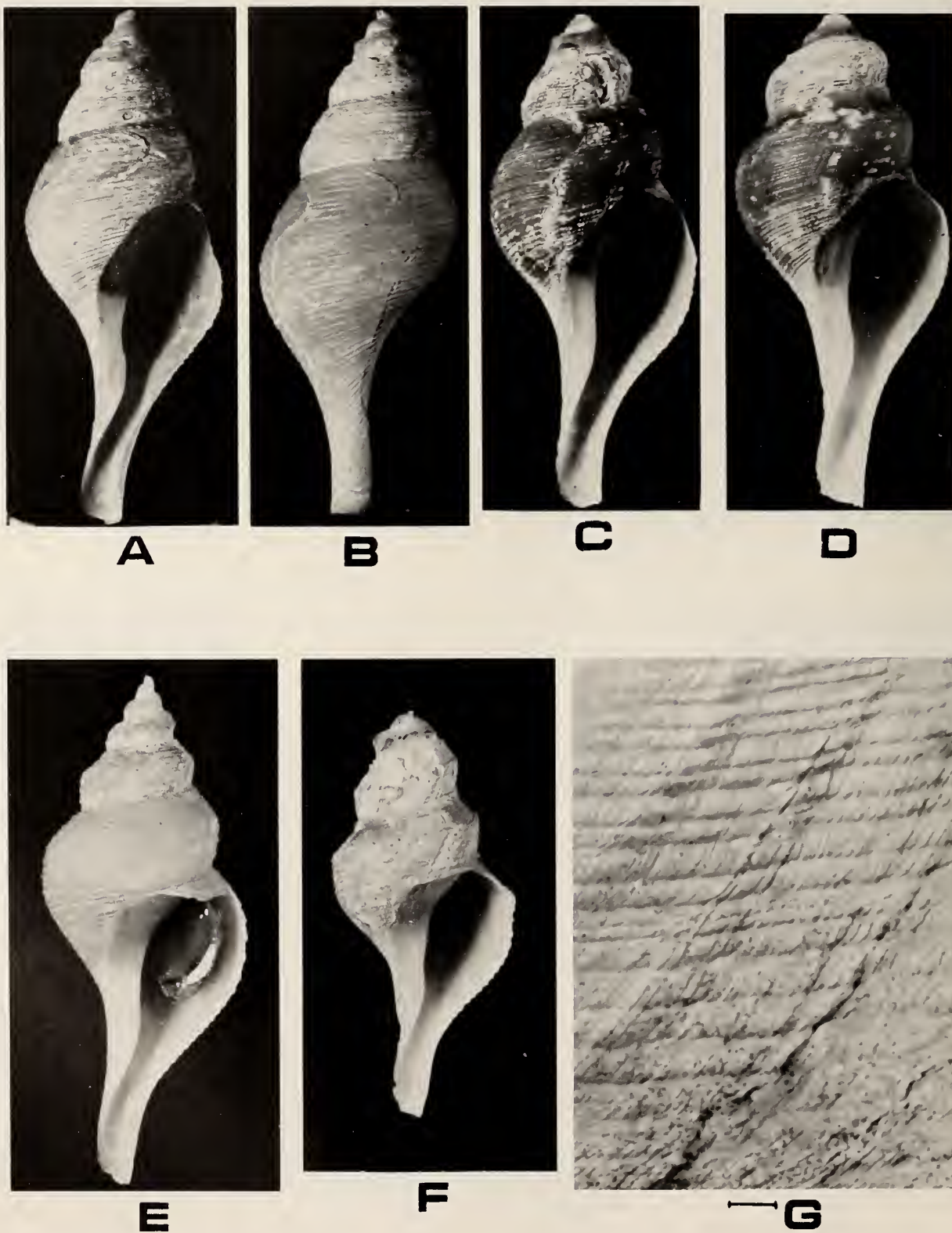
Figure 2

A–G, *Aforia abyssalis* sp. nov. A and B, holotype. C, paratype, R/V *Vityaz,* stat. 5624, shell height of 31.8 mm. D, paratype, R/V *Vityaz,* stat. 5624, shell height of 31.0 mm. E, paratype, R/V *Vityaz,* stat. 3594, shell height of 39.0 mm. F, paratype, R/V *Vityaz,* stat. 4104, shell height of 16.8 mm. G, paratype, shell sculpture. Scale bar = 1 mm.
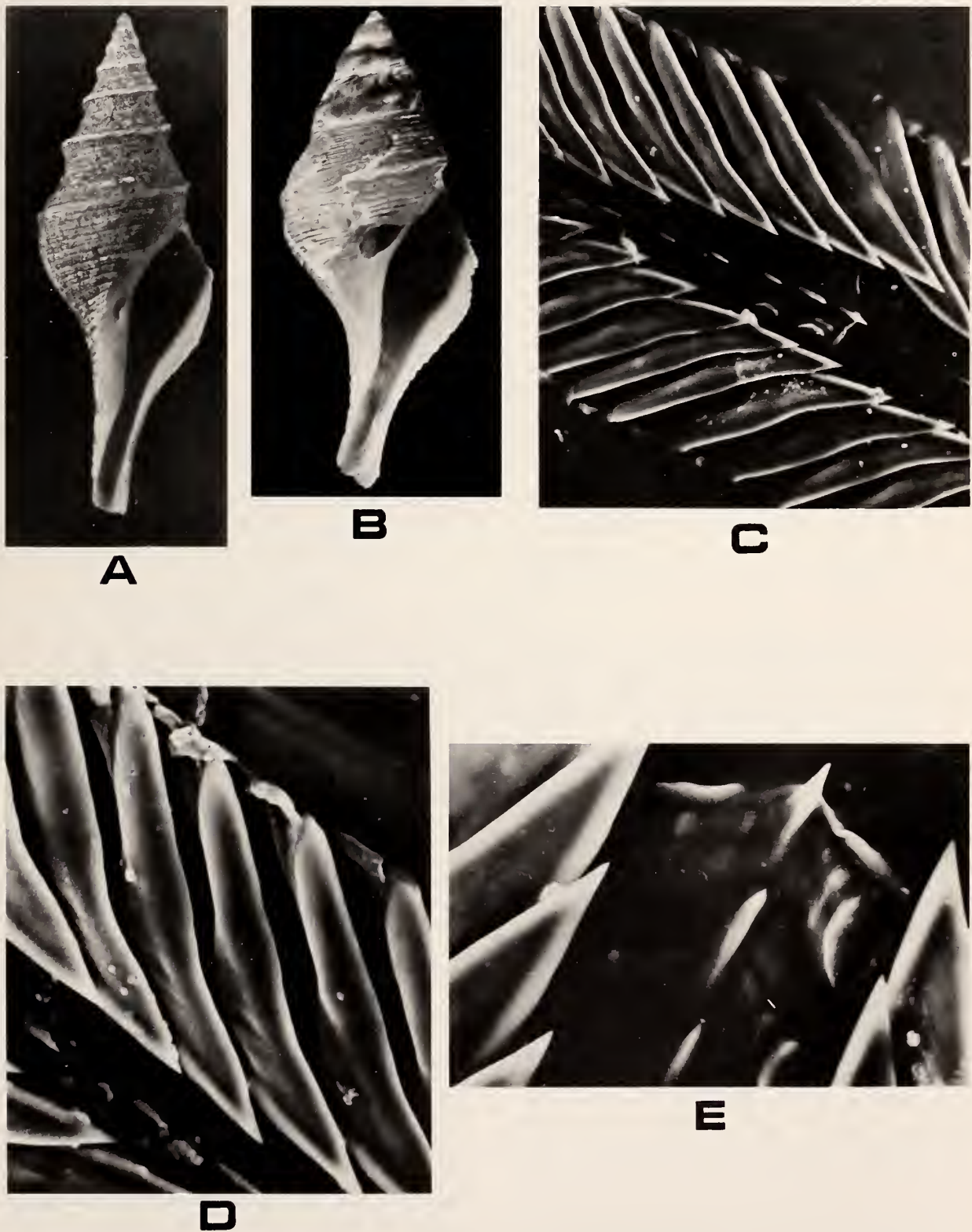
Figure 3

A, *Aforia circinata* (Dall), shell height of 52.4 mm. B, *A. aulaca alaskana* subsp. nov., holotype. C–E, SEM photographs of radula of *A. circinata*.
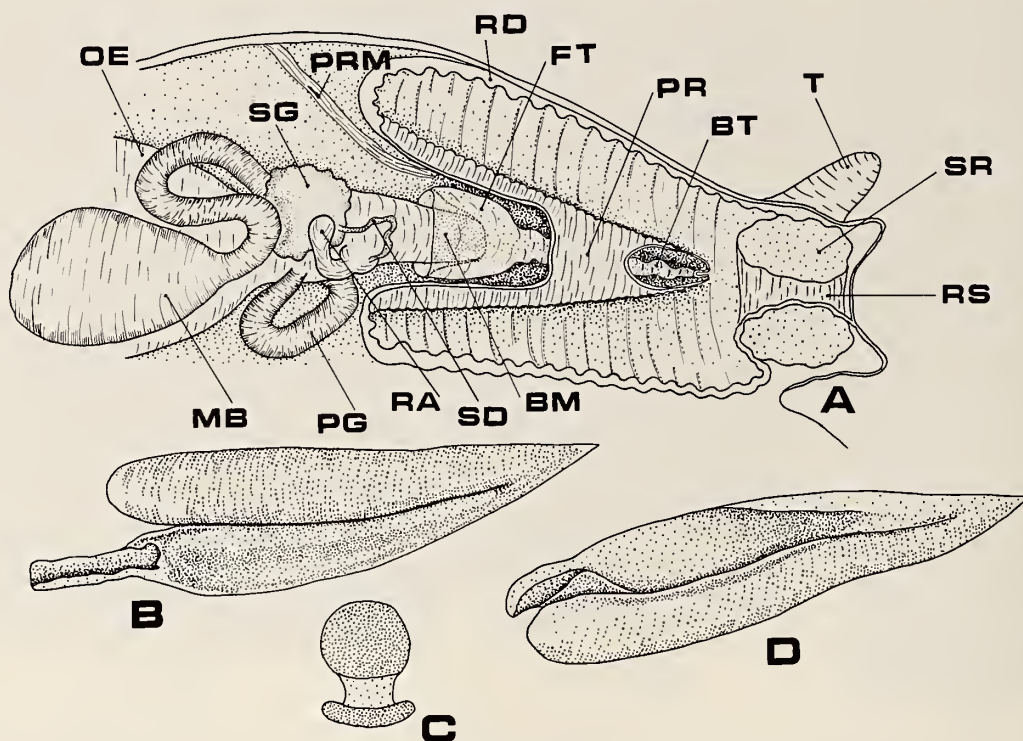
Figure 4

A, general diagrammatic section of the anterior part of *Aforia* digestive sytem. B–D, marginal teeth of *Aforia* (B, *A. circinata*. C, the same, transverse section. D, *A. abyssalis*). Key to abbreviations for all figures: AG, accessory pedal gland; AO, anal opening; BT, buccal tube; BM, buccal mass; BW, body wall; CT, central tooth; DG, digestive gland; FT, fold of buccal tube; FG, female gonopore; G, gill; H, head; HG, hypobranchial gland; LM, longitudinal muscles; LR, lip of rhynchostome; MB, muscular bulb; MG, male gonopore; MT, marginal tooth; N, nephridium; OC, odontophoral cartilage; OE, oesophagus; OP, operculum; OS, osphradium; PG, poison gland; PO, pallial oviduct; PR, proboscis; PRM, retractor muscles of the proboscis; PP, propodium; PS, proboscidal sphincter; RA, radula; R, rectum; RD, rhynchodaeum; RS, rhynchostome; RT, radular tooth; S, siphon; SD, salivary duct; SG, salivary gland; SP, sublingual pouch; SR, rhynchostomal sphincter; ST, stomach; T, tentacles; TM, transverse muscles.

the anal sinus of the shell. The head is well distinguished from the body. The tentacles are long and flattened. The propodium is very narrow, and the accessory pedal gland is poorly developed. A large rhynchostomal sphincter is present.

Mantle complex (Figure 6C): The gill and osphradium are large, the latter being ⅔ of the gill length. Gill lamellae are tall and triangular. The thickened flagellum of the gill is free in its upper part to form a rounded growth. The hypobranchial gland is well developed, and forms about 30 closely placed folds. A long siphon with a large distributive valve at its base is well developed. The rectum is of small diameter with a small but distinct anal papilla.

Digestive system (Figure 9): The proboscis is long, narrowing towards its tip. Powerful proboscis retractor muscles are attached mostly to the integument of the body sinus roof. The buccal mass is not large. The buccal tube is surrounded with a relatively thin layer of circular mus-

culature to form a long double fold along the buccal mass. There is a small sphincter of the buccal tube at its tip in which a radular marginal tooth was found to be held (Figure 9B). The muscular bulb of the poison gland is rather small and oval. The salivary glands join to form a single gland placed above the oesophagus and embracing it. The salivary ducts are relatively thick and twist slightly. The odontophore is small (Figure 9C); there are four subradular cartilages forming pairs on each side. The paired cartilages fuse in the anterior part of the odontophore and the fused pairs are connected with a muscular symphysis. The radular sac is lined with a thick layer of cuticle. The rachidian tooth of the radula is thin, weak, and curved, with a smooth anterior edge. The marginal teeth (Figures 9D, E) are short, broad, and their distal parts are optically more dense than the basal parts. The length of a marginal tooth is 0.24 mm. The shell height - tooth length ratio is 113.3. The oesophagus abruptly widens behind the entrance of the poison gland. The stomach is of the typical

U-shape, with two ducts of the digestive gland. The specimen dissected is an immature female.

Remarks: This species is closest to *Aforia **kupriyanovi*** sp. nov., differing by the weak development of spiral ribs on the body-whorl shoulder, the lesser number of ribs, the flattened whorl shoulder, and the much smaller marginal teeth (as measured in relative values).

Distribution: The species was found in the abyssal zone of the region southward from the Hyort trench (southwestern Pacific).

Subgenus *Steiraxis* Dall, 1896

Type species: *Pleurotoma (Steiraxis) aulaca* Dall, 1896 (O.D.).

Spiral sculpture consists of very strong, prominent, nearly rectangular in section ribs equally developed throughout the shell surface. The spiral keel is strong and situated at the whorl periphery. Marginal teeth of the radula are very large, and the shell height–tooth length ratio is about 70.

The subgenus includes a single species with two subspecies (*Aforia aulaca aulaca* (Dall) and *A. aulaca **alaskana*** subsp. nov.) living at abyssal depths of the eastern Pacific along the coast of North and Central America.

*Aforia (Steiraxis) aulaca **alaskana***
Sysoev & Kantor, subsp. nov.

(Figures 3B, 5D, 12F–H)

Material: R/V *Vityaz,* station 6109, 56°17.7′N, 139°43.3′W (Gulf of Alaska), depth 3460 m, Sigsbee trawl, 1 specimen (holotype, No. LC 5362).

Description of holotype: The shell is small, fusiform, and consists of 5 whorls. The upper whorls are significantly eroded. The whorls are slightly convex, angled at the periphery where a spiral keel is placed. The whorls are divided by very shallow, poorly visible sutures. The whorl shoulder is flattened. Axial sculpture is represented only by very thin, numerous growth lines. Spiral sculpture consists of the keel situated at the whorl periphery and also of strong, prominent, nearly rectangular in section ribs covering all the shell surface. The width of ribs varies insignificantly. Sometimes, there is an additional thin rib in the interspace between the more prominent ribs. There are two ribs on the spiral keel. The ribs are much lower on the shell base and on the anterior canal. Interspaces between ribs vary in their width, being in most cases equal to the ribs themselves or slightly wider. There are 15 spiral ribs on the penultimate whorl and 48 on the body whorl; 11 of the latter are disposed between the keel and the suture. The ovate aperture gradually transforms into the long siphonal canal, which is slightly curved and widens toward the end. The inner lip is coated with a wide but thin callus. The anal sinus, judging by growth lines, is wide, rounded, and not very deep, its apex being placed approximately in the middle of the space between the
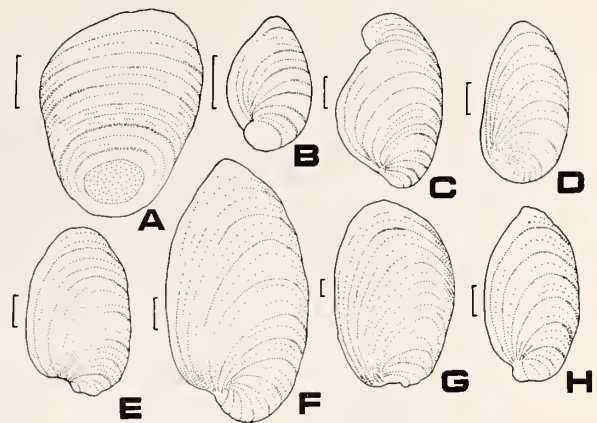

Figure 5

Opercula of *Aforia* species. A, *A. **moskalevi***, paratype. B, *A. lepta*. C, *A. crebristriata*. D, *A. aulaca **alaskana***, holotype. E–G, *A. abyssalis* (E, paratype, R/V *Vityaz,* stat. 5624. F, paratype, R/V *Vityaz,* stat. 3594. G, paratype, R/V *Vityaz,* stat. 2074). H, *A. **kupriyanovi***, holotype. Scale bar = 1 mm.

suture and the keel. The shell color is light brown. The shell height is 25.8, the body-whorl height is 20.0, the height of the aperture is 16.5, and the shell diameter is 11 mm.

Anatomy: The rhynchostomal sphincter is very poorly developed, compared to other species. The rhynchostome has weak, small rhynchostomal lips. A small accessory propodial gland is placed on the bottom of the propodial cleft.

Mantle complex of organs: The mantle morphology is typical for the genus. The mantle edge is serrated. The ctenidial lamellae are high, and there is a thick cuticular basal flagellum at the inner edge. The hypobranchial gland is poorly developed.

Digestive system: The proboscis (Figure 12F) is typical for the genus. The buccal mass is small, and the buccal tube is surrounded by a rather thick layer of circular musculature. Near the tip of the proboscis the buccal tube forms a sphincter (Figure 12G). Powerful and large proboscis retractors are attached to the expansion of the buccal tube at some distance from the proboscis tip. It is possible that the end of the buccal tube can be everted. The poison gland is thick and has a very large muscular bulb. The central radular tooth is large; it has one cusp on its frontal edge and long, narrow, curved blades (Figure 12H). The marginal teeth are long and slightly curved (Figure 12H) (0.38 mm length). The shell height–tooth length ratio is 67.9.

Remarks and distribution: *Aforia aulaca **alaskana*** subsp. nov. differs from the nominal subspecies in having a smaller shell (the height of holotype shell of *A. aulaca aulaca* is 60 mm) that is covered with spiral ribs that are not sharp
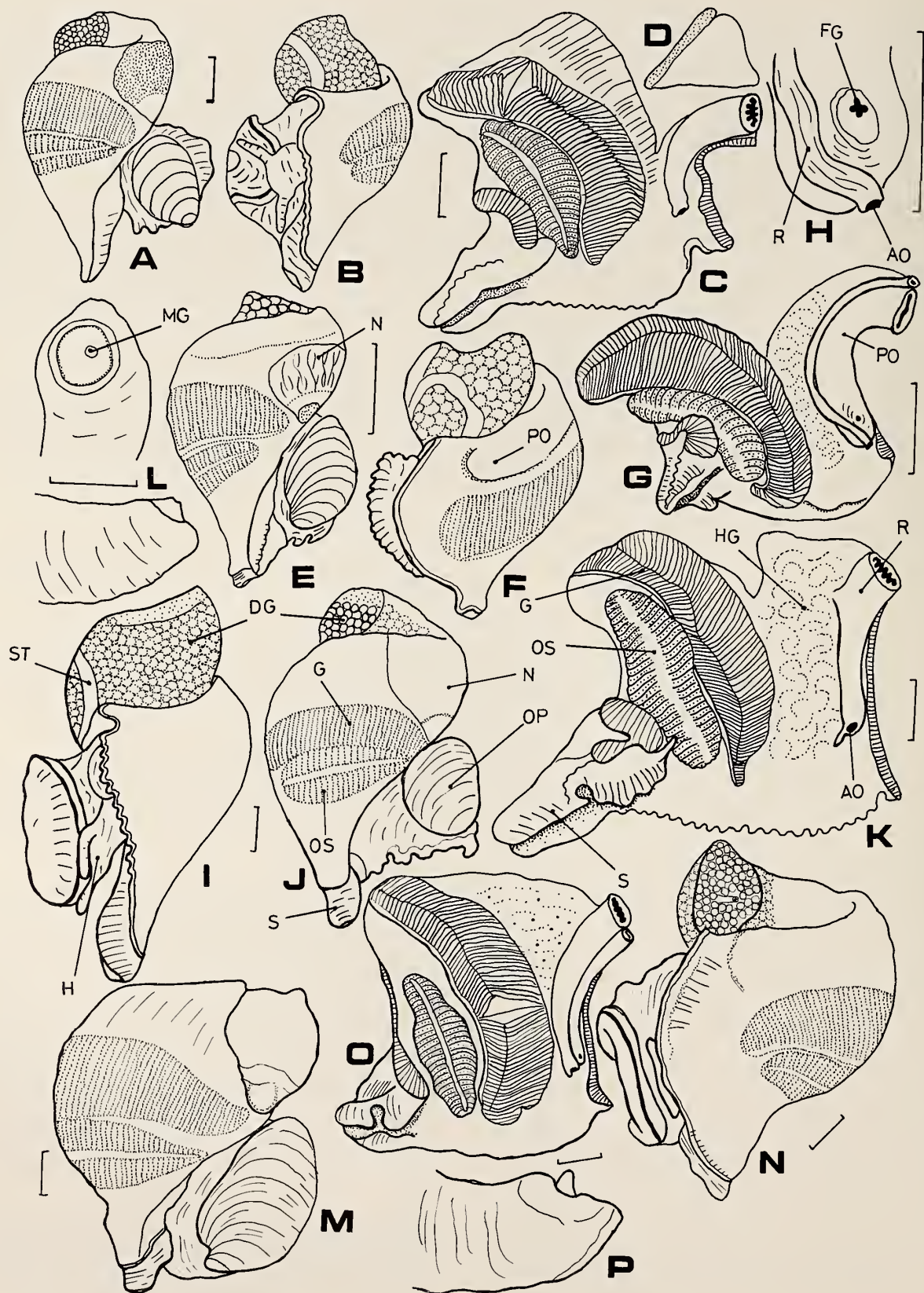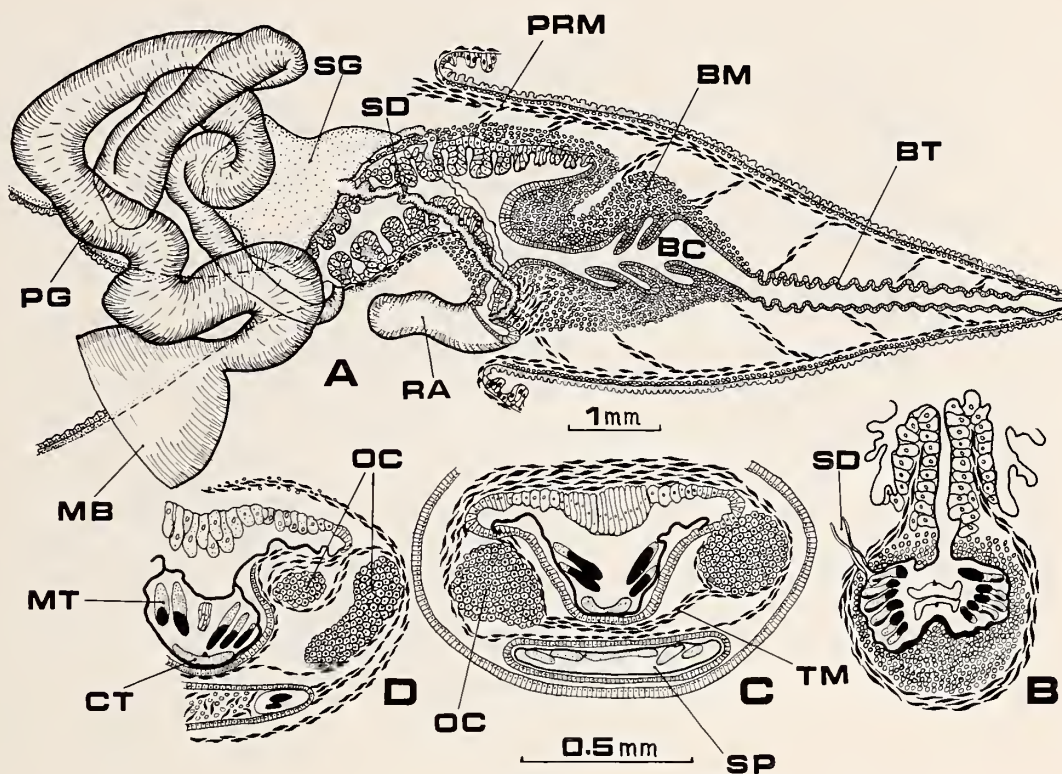
Figure 7

Morphology of digestive system of *Aforia circinata,* shell height of 49.0 mm. A, semidiagrammatic section of anterior part of digestive system. B, transverse section across the radular sac at the anterior part of odontophore. C, the same, medial part of odontophore. D, the same, basal part of odontophore. See Figure 4 for key to abbreviations.

but rectangular in side view, and with interspaces between them being equal or slightly wider than the rib width (*i.e.,* the interspaces between ribs are wider than in the nominal subspecies). The most striking difference between the subspecies is the shape of the radular teeth. The drawing of the radula of the holotype specimen of *A. aulaca aulaca* (according to the catalogue number) was published by POWELL (1966:text fig. 26). The marginal teeth of the new subspecies are wider; the central tooth is large and crescentlike with a cusp on its frontal edge whereas the central tooth of the nominal subspecies is represented by a narrow small plate that is protracted along the subradular membrane and bipolarly sharply terminating. Moreover, the two subspecies differ in their geographic distribution. *Afor-*

ia aulaca aulaca is found along the Pacific coast of North and Central America from northern California to the Gulf of Panama (DALL, 1908; PARKER, 1964; ROKOP, 1972). *Aforia aulaca* **alaskana** has been recorded so far only in the Gulf of Alaska. It is interesting to note that both subspecies have a similar vertical range, 3241–3798 and 3460 m respectively.

Subgenus *Dallaforia*
Sysoev & Kantor, subgen. nov.

Type species: *Irenosyrinx? crebristriata* Dall, 1908.

Spiral sculpture is represented by very strong, wide, prominent ribs situated below the whorl shoulder and

Figure 6

Soft body of *Aforia* species. A–D, *A. moskalevi,* paratype (A and B, whole body. C, mantle complex. D, single lamella of the gill). E–H, *A. lepta* (E and F, whole body. G, mantle complex. H, distal part of female pallial gonoduct and rectum). I–L, *A. crebristriata* (I and J, whole body. K, mantle complex. L, penis). M–P, *A. abyssalis,* paratype, shell height of 39.0 mm (M and N, whole body. O, mantle complex. P, penis). Scale bar = 2 mm. See Figure 4 for key to abbreviations.
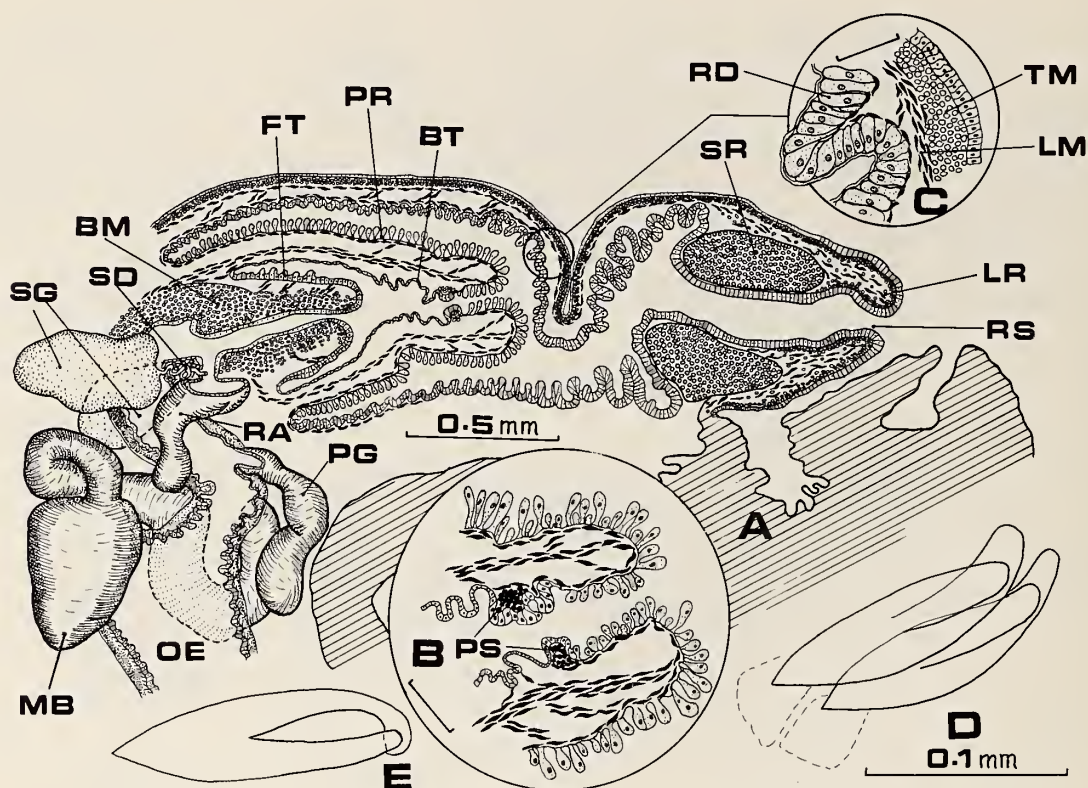
Figure 8

Morphology of digestive system of *Aforia lepta*. A, semidiagrammatic section of anterior part of body (the foot is hatched). B, magnified tip of the proboscis. C, magnified part of body wall. D and E, radula. Scale bar for B and C = 0.1 mm. See Figure 4 for key to abbreviations.

weak, flattened ribs on the shoulder. A spiral keel is absent. Marginal teeth of the radula are of middle size, and the shell height–tooth length ratio about 100.

The subgenus is represented only by the type species living in abyssal regions of the northeastern Pacific.

Aforia (*Dallaforia*) *crebristriata* (Dall, 1908)

(Figures 1A, B, 5C, 6I–L, 10A–C)

Irenosyrinx? crebristriata DALL, 1908:272, pl. 13, fig. 10.

Material: R/V *Vityaz*, station 4173, 44°54′N, 128°32′W (off Oregon), depth 2830–2840 m, trawl Sigsbee, 3 specimens.

A detailed description of the shell of *Aforia crebristriata* was given in the original description of the species. Therefore, we add data only on the operculum, anatomy and radula, which are absent in Dall's article.

Operculum: The operculum is small in comparison with other species of the genus; its shape is nearly triangular, with a terminal nucleus. The part most remote from the nucleus of the operculum of one of our specimens has a rounded projection (Figure 5C) that appears the probable result of a disturbance during its growth.

Anatomy (Figures 6I–L): The studied specimen has a shell height of 30.0 mm. The tentacles are long and cylindrical. The propodium is very narrow; the marginal cleft is shallow. The accessory pedal gland is poorly developed. At both sides of the propodium base, the metapodium forms rather long and large palps. The mantle is thin and the osphradium and gill are clearly seen through it. The mantle edge is scalloped; its projections correspond to spiral ribs. The mantle does not cover the head base.

Mantle complex (Figure 6K): The osphradium and the gill are large. The narrow gill is formed by tall triangular lamellae. The basal flagellum is weakly thickened and attached to the lamella along nearly its entire length. The gill axis is very thin. The osphradium is greenish. The hypodermal gland is covered with a thick layer of gel-like mucosa. The siphon is long and has a small distributive valve at its base. The rectum is of small diameter; there is a small palp formed by the rectal wall.

Digestive system (Figure 10): The proboscis is long. The buccal mass has rather thin walls. The buccal tube is surrounded by a moderately thick layer of circular muscles; it forms a long fold along the buccal mass. Salivary glands unite as one gland located above the oesophagus. The
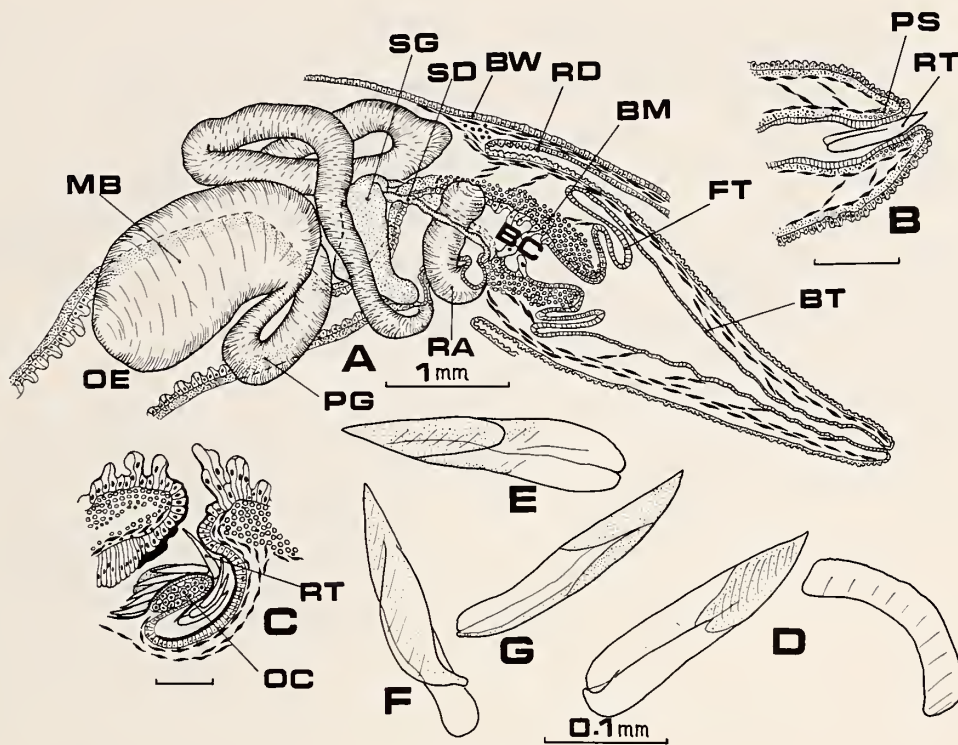
Figure 9

Morphology of digestive system of *Aforia moskalevi*, paratype. A, semidiagrammatic section of the anterior part of digestive system. B, magnified tip of the proboscis. C, longitudinal section across the anterior part of radular sac. D, radula in natural position. E–G, marginal tooth, various projections. Scale bar for B and C = 0.2 mm. See Figure 4 for key to abbreviations.

salivary ducts are paired and of small diameter. Two odontophoral cartilages are very large; they unite in the anterior part of the odontophore (Figure 10B). The epithelium of the radular sac and the buccal cavity is lined with a thin cuticular layer. The large proboscis retractor muscles are placed near the proboscis walls and attach to the proboscis wall near its tip. The muscular bulb of the poison gland is large. The oesophagus abruptly widens behind the nerve ring. The poison gland opens into the oesophagus rather far from the radular sac. The radular sac is surrounded by a thick muscular layer. The central radular tooth has moderately wide, nearly straight, and almost rectangular blades, and one thin and long cusp on the frontal edge. The marginal teeth are wide, short, slightly curved, and very small (their length is 0.29 mm when the shell height is 30.2 mm). The shell height–tooth length ratio is 104.1. The stomach is of the typical U-shape, and contains paired closed ducts of the digestive gland.

Reproductive system: The vesicula seminalis is very large, formed by numerous very small loops of the seminal duct. The penis is relatively short and broad (Figure 6L), with slightly folded walls. The genital papilla is large, rounded, and surrounded by a circular fold. The male gonopore opens somewhat laterally in a small invagination.

Distribution: The species inhabits the upper abyssal zone along the northwestern coast of North America from the Gulf of Alaska to Oregon at depths of 2830 to 2869 m. Type locality—station 2859 of R/S *Albatross* (off Sitka, Alaska).

Subgenus *Abyssaforia*
Sysoev & Kantor, subgen. nov.

Type species: *Aforia* (*Abyssaforia*) *abyssalis* Sysoev & Kantor, sp. nov.

Spiral sculpture is represented by numerous narrow, prominent ribs equally developed throughout the shell surface. A spiral keel is absent or a trace is retained as a slight angulosity of the whorl shoulder visible on early whorls. Marginal teeth of the radula are large, and the shell height–tooth length ratio is less than 100 (57–90).

Representatives of the subgenus live in abyssal regions of the Pacific and the northern Atlantic.

The subgenus includes three species—*A. abyssalis* Sysoev & Kantor, sp. nov., *A. hypomela* Dall, 1889, and *A. kupriyanovi* Sysoev & Kantor, sp. nov.

Most deep-water species of *Aforia s.s.* possess spiral sculpture close to that of *Abyssaforia*.
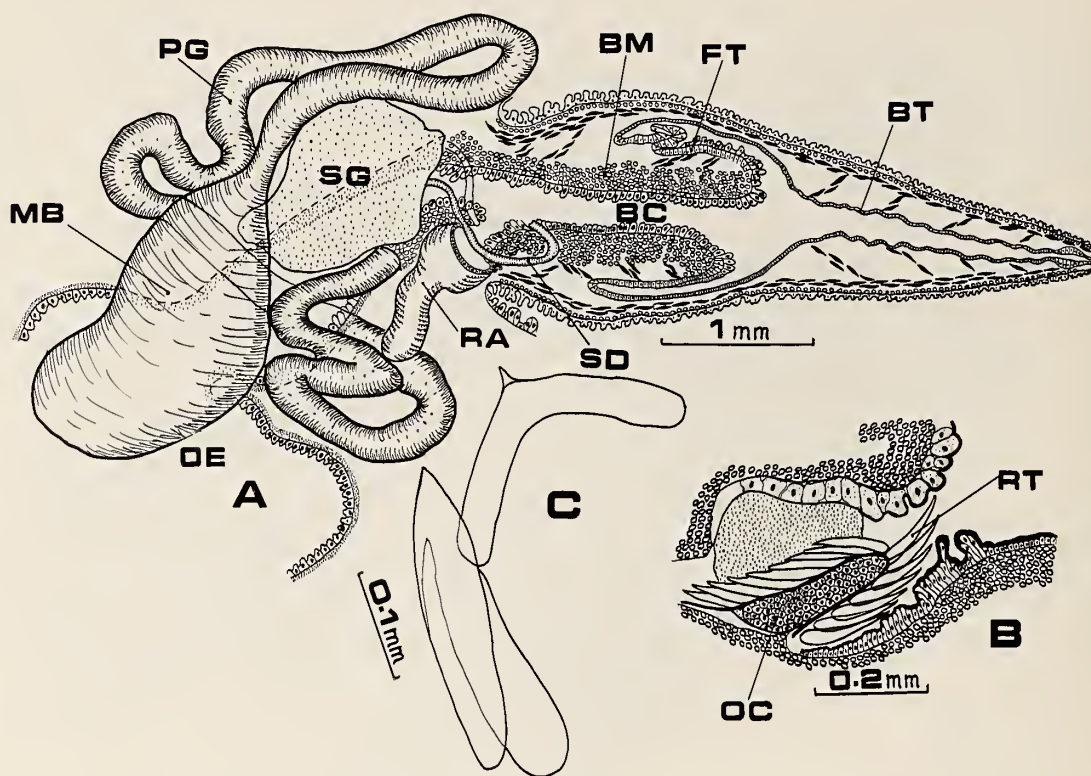
Figure 10

Morphology of digestive system of *Aforia crebristriata*. A, semidiagrammatic section of the anterior part of digestive system. B, longitudinal section across the anterior part of radular sac. C, radula. See Figure 4 for key to abbreviations.

Aforia (Abyssaforia) abyssalis
Sysoev & Kantor, sp. nov.

(Figures 2A–G, 4D, 5E–G, 6M–P, 11A–F)

Material: R/V *Vityaz,* station 2074, 42°32′N, 150°41′E (SE of Iturup, Kurile Islands), depth 5140 m, trawl Sigsbee, 2 specimens; station 2119, 46°07.8′N, 155°16′E (E of Urup, Kurile Islands), depth 5070–5090 m, trawl Sigsbee, 1 specimen (holotype, No. LC 5363); station 3594, 40°55.2′N, 144°53.3′E (SE of Hokkaido, Japan), depth 3880–3900 m, trawl Sigsbee, 1 specimen and 1 shell; station 4104, 41°07.5′N, 159°53.9′W (NE Pacific), depth 5430–5456 m, trawl Sigsbee, 1 juvenile specimen; station 5624, 45°26′N, 154°12′E (E of Urup, Kurile Islands), depth 5220 m, trawl Galathea, 22 specimens (mostly juveniles) and 1 shell. All the paratypes are stored as No. LC 5364.

Description of holotype: The shell is medium in size for the genus, elongately fusiform, thin, and consists of 5 preserved whorls. The protoconch and upper whorls are seriously eroded. Whorls are weakly convex, somewhat angled at the periphery; the whorl shoulder is flattened. Axial sculpture is represented by growth lines that are numerous, clear, and very thin; some of them, probably reflecting

significant interruptions of shell growth, clearly differ from others in their prominence. There are 6 of these growth lines on the body whorl. Spiral sculpture consists of thin, clear, pronounced, cordlike ribs separated by always larger interspaces. The ribs are separated from each other by uneven intervals; they are closest at the periphery of the whorl where the interspaces are 1.5–2 times wider than the width of the rib itself. They are most distant from each other on the whorl shoulder where interspaces are 3–7 times wider than those of the ribs. On the body whorl, 1 or 2 weak, thin accessory ribs may be situated in the interspaces. There are 15 spiral ribs on the penultimate whorl and about 60 on the body whorl, including the canal. The aperture is narrow and ovate; its outer lip is thin. The inner lip is gradually curved, covered by translucent callus, and develops a small projection when passing into the canal. The canal is long and curved. The shell color is grayish cream. The height of the shell is 56.3 mm, the height of the body whorl is 43.0 mm, the height of the aperture is 35.1 mm, and the shell diameter is 21.0 mm.

Younger paratype specimens are characterized by more convex and angled shell whorls. A tendency can be noted in some young specimens to develop a slight fold at the upper part of the whorl near the suture. The spiral ribs
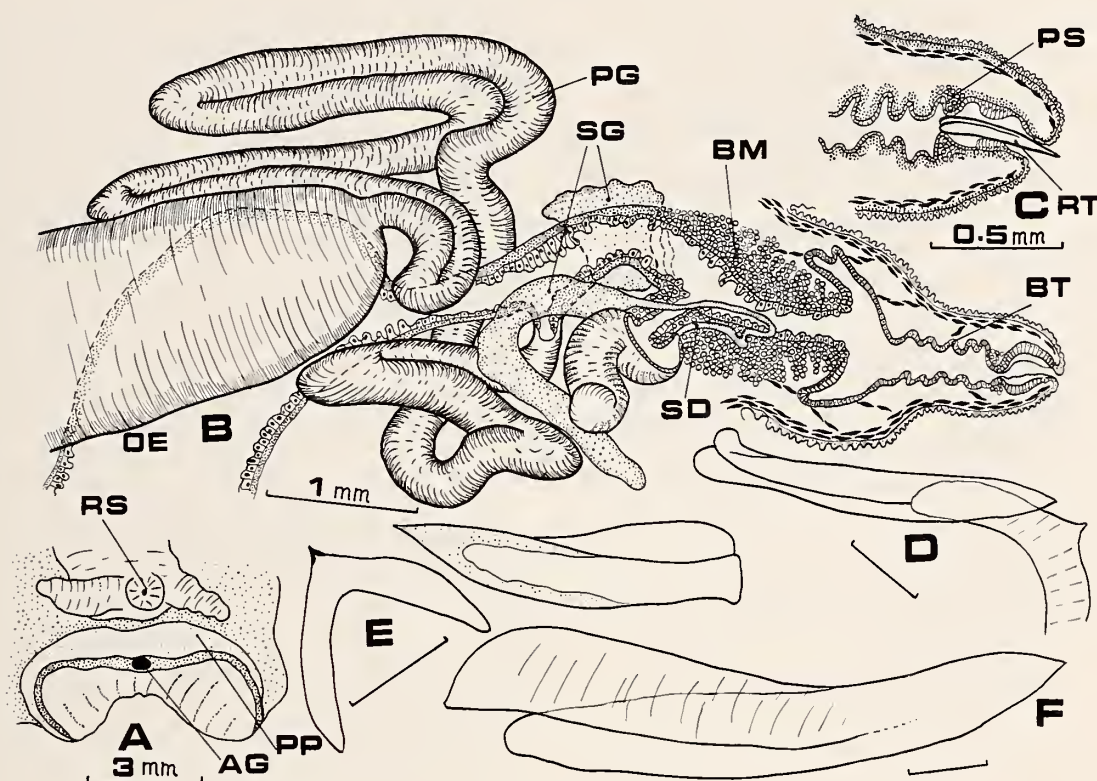
Figure 11

Morphology of digestive system of *Aforia* **abyssalis**, paratype, shell height of 39.0 mm. A, head. B, semidiagrammatic section of the anterior part of digestive system. C, magnified tip of the proboscis. D, radula of paratype (R/V *Vityaz*, stat. 3594, shell height of 39.0 mm). E, the same (R/V *Vityaz*, stat. 5624, shell height of 25.7 mm). F, marginal tooth of paratype (R/V *Vityaz*, stat. 2074, shell height of 74.2 mm). Scale bar for D–F = 0.1 mm. See Figure 4 for key to abbreviations.

in paratypes, especially in young ones, sometimes are more flattened, wider, and closer to each other, especially on the whorl shoulder. The growth lines of smaller shells, particularly on upper whorls, may be more rough, prominent, and can form some kind of weak axial folds on the shell surface. The shell height of the largest paratype is 74.2 mm.

The operculum is ovate and large (Figures 5E–G).

Anatomy (Figures 6M–P): (The anatomy of a paratype from station 3594, having a shell height 39.0 mm, is shown in the most Figures except 6P). The propodium is narrow, and the marginal cleft is not deep. The accessory pedal gland is situated almost at the central part of the cleft. The mantle completely covers the head, which is well distinguished from the body. Tentacles are cone-shaped and rounded at the tip. The rhynchostomal lips form a funnel. The rhynchostome is small; its large and powerful sphincter constitutes the major part of the head volume.

Mantle complex (Figure 6O): The gill is very large; its length is nearly equal to the mantle length. The lamellae

are tall and triangular, with poorly thickened lamellae at their inner sides which completely adhere to the lamellae. The osphradium is of medium size, and greenish. The hypobranchial gland forms inconspicuous folds covered with a thick layer of gel-like mucus. The rectum is of small diameter, and its wall forms a small palp near the anus.

Digestive system (Figure 11): The proboscis is rather short. The buccal mass is large and has thick walls. The buccal tube forms a small fold along the buccal mass. The salivary gland is paired; the right salivary gland is elongate and the left one is more ovate. The salivary ducts are slightly coiled, moderately thick, and open into the radular sac near its entrance into the buccal cavity. The odontophoral cartilages are very thin, narrow, and connected in the anterior part by a transverse muscle. There are 4 cartilages, which are united in 2 pairs. The muscular bulb of the poison gland is very large with a small lumen. The oesophagus gradually widens behind the opening of the poison gland. The stomach is of the typical U-shape and contains a single duct of the digestive gland. The radular
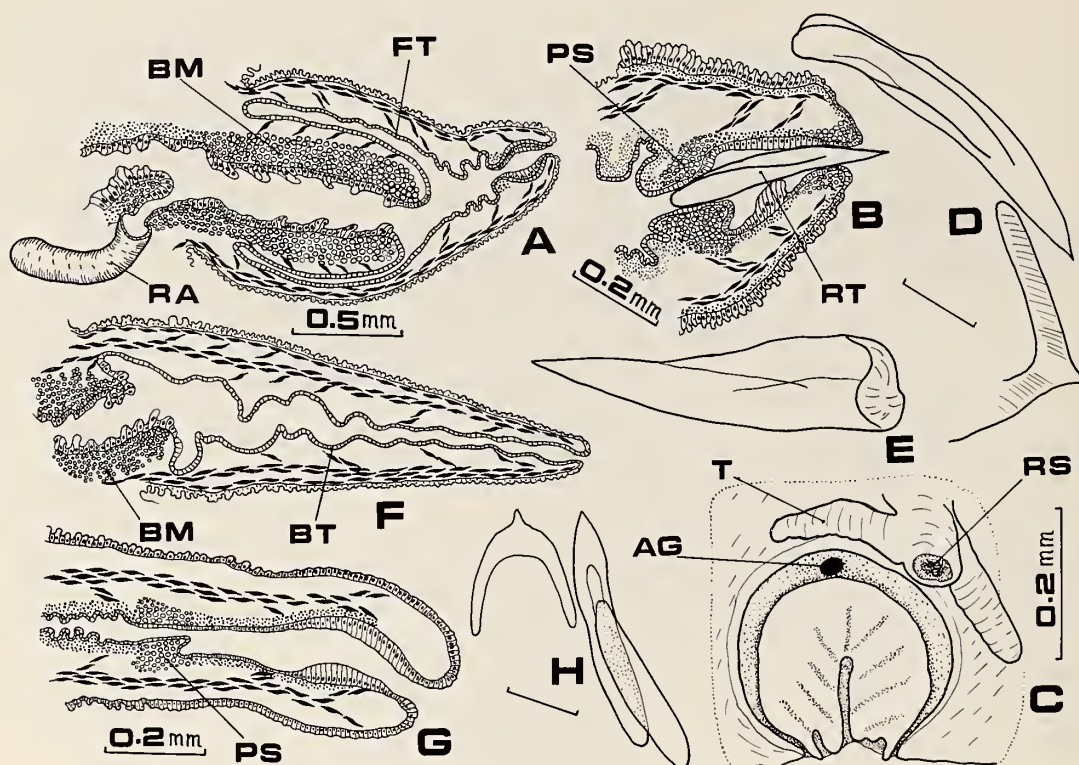
Figure 12

A–E, *Aforia kupriyanovi,* holotype. A, semidiagrammatic section of the proboscis. B, magnified tip of the proboscis.
C, head and the anterior part of the foot. D, radula. E, marginal tooth in lateral projection. Scale bar for D and
E = 0.1 mm. F–H, *A. aulaca alaskana,* holotype. F, semidiagrammatic section of the proboscis. G, magnified tip
of the proboscis. H, radula. Scale bar = 0.1 mm. See Figure 4 for key to abbreviations.

teeth show variability based on age. The younger specimen
has more short and broad marginal teeth (Figure 11E)
than the older one (Figure 11F). The central tooth has
one cusp which becomes sharper and longer during growth
of the mollusk. The length of the marginal tooth of the
specimen with the shell height of 25.7 mm is 0.30 mm,
with the shell height of 39.0 mm it is 0.44 mm, and with
the shell height of 74.2 mm it is 0.80 mm. The shell height–
tooth length ratios are 82.9, 88.6, and 90.5 respectively.

Reproductive system: One of studied paratypes (station
3594) is an immature female. The paratype from station
5624 is a mature male. Its vesicula seminalis is very large,
with numerous small loops of seminal duct. The penis
(Figure 6P) is long, flattened, and sharp at the frontal
edge. The male gonopore opens on a small papilla sur-
rounded with a circular fold.

Remarks: The species is conchologically very close to *Afor-
ia hypomela* Dall, differing in that the new species has
more numerous and narrow spiral ribs, a more curved
siphonal canal, different form and size of the radular teeth
(for *A. hypomela* see BOUCHET & WAREN, 1980:fig. 7),
and a different geographical distribution: *A. hypomela* is

an Atlantic species while *A. abyssalis* sp. nov. is presently
reported only from the Pacific.

Distribution: The species inhabits the lower abyssal zone
of the northern Pacific at depths of 3880 to 5456 m; most
records are from the northwestern Pacific.

Aforia (Abyssaforia) kupriyanovi
Sysoev & Kantor, sp. nov.

(Figures 1C, D, 5H, 12A–E)

Material: R/V *Akademik Kurchatov,* station 240, 23°47′S,
71°03′W, (off Antofagasta, Chile), depth 4300 m, trawl
Galathea, 1 specimen (holotype, No. LC 5365).

Description of holotype: The shell is of moderate size,
fusiform, thin, fragile, and consists of 5.5 preserved whorls.
A part of the protoconch is lost; the upper whorls are
seriously eroded. The shell whorls are convex, rounded,
and separated from each other by definite shallow sutures.
The body whorl occupies about ¾ of the shell height.
Growth lines are weak and poorly visible. The spiral sculp-
ture consists of similar, low, cordlike, slightly wavy ribs
covering all the shell surface and separated from each other

by interspaces that are 2–4 times wider than the ribs. The ribs are placed more closely to each other at the whorl periphery and more distant at the shell base. Two ribs of the periphery of the body whorl are situated on a weak eminence and look like a very poorly developed spiral keel. There are 15 ribs on the penultimate whorl and 44 on the body whorl including the canal. The aperture is wide and ovate. There is a large, low knob at the upper portion of the inner lip. The canal is long and curved. The anal sinus, judging by growth lines, is wide, deep, and rounded. The shell color is grayish white. The shell height is 26.4 mm, the body-whorl height is 19.9 mm, the aperture height is 16.2 mm, and the shell diameter is 11 mm.

The operculum is ovate; its growth axis is strongly curved.

Anatomy: The propodium is narrow, the marginal cleft is not deep, and the accessory pedal gland is situated at its middle part. Diameter of the pedal gland is about 0.25 mm. The metapodium forms small palps at both sides of the propodial base (Figure 12C). The head is elongate and well distinguished from the body. The tentacles are long and cylindrical. The rhynchostome is wide; its sphincter is large.

The mantle complex is typical for the genus. The osphradium and the gill are large, and the mantle edge forms a deep notch, corresponding to the anal sinus of the shell. The distributive valve of the siphon is small. The gill lamellae are tall, with a thickly cuticulized flagellum.

Digestive system: The proboscis is not large (Figure 12A). The buccal mass is very large; its length exceeds ½ of the proboscis length. The buccal tube forms a very long fold along the mass. The buccal tube is surrounded by a rather thick layer of circular muscles. At the tip of proboscis, the buccal tube forms a small enlargement in which a single radular marginal tooth was found to be held (Figure 12B). The tooth basal part is held by the sphincter that is situated at the base of the enlargement. Another sphincter is at the tip of the proboscis. The retractor muscles of the proboscis are rather small; they follow along the proboscis walls. The buccal tube is connected with the proboscis walls by numerous muscles. The central radular tooth has long curved blades and one broad cusp on the frontal edge. The marginal teeth are curved (Figures 12D, E), rather broad, and small (0.46 mm). The shell height–tooth length ratio is 57.4. The muscular bulb of the poison gland is large, and elongate–oval. The stomach is of the typical U-shape, containing two ducts of the digestive gland.

Remarks: The species is most similar to the abyssal species *Aforia hypomela* Dall and *A. abyssalis* sp. nov., but differs clearly by having a small shell, with rounded, strongly convex whorls, stronger spiral ribs, and a long, considerably curved siphonal canal, and different radular tooth (especially the central one) form.

Distribution: The species lives in the abyssal zone of the Peru-Chilean trench.

Subgenus *Palaeoaforia*
Sysoev & Kantor, subgen. nov.

Type species: *Aforia campbelli* Durham, 1944.

Spiral sculpture consists of slight, narrow ribs that are smoothed on the whorl shoulder and of two strong spiral keels on the lower part of the whorl shoulder and on the shell base.

The subgenus is represented mostly by fossil species (*Aforia campbelli* Durham, 1944, *A. wardi* (Tegland, 1933), *A. addicotti* Javidpour, 1973, *A. clallamensis* (Weaver, 1916), *A. tricarinata* Addicott, 1966) reported from Oligocene and lower Miocene deposits of western North America (JAVIDPOUR, 1973). *Aforia trilix* (Watson, 1886) is the only Recent species that can be probably included in this subgenus. Nevertheless the species' taxonomic position (including its belonging to *Aforia*) at present is uncertain and needs further investigations.

An opinion on the possibility of isolating Oligocene *Aforia* as a separate subgenus was earlier expressed by HICKMAN (1976) based on the presence of the second keel on Oligocene shells.

DISCUSSION

General Morphology of Species of *Aforia*

Generally the organ morphology of studied systems is very similar among subgenera and species of *Aforia*. We could not find any significant differences at the subgeneric level. The digestive system manifests probably the most marked differences between species.

The rhynchodaeum, the wall of the proboscis sheath, is folded in all species; its epithelium is represented by tall secretory cells. In most species, the rhynchodaeum adheres to the wall of the body haemocoel whereas in *Aforia lepta* it is free all along its length to be connected only in places to the haemocoel wall with thin muscles. An invaginable part of the rhynchodaeum, such as is present in gastropods with a pleurembolic proboscis, is absent in *Aforia*. However, most *Aforia* species can stretch the proboscis out of the rhynchostome. This process is facilitated by secretions produced by the secretory epithelial cells lining the proboscis and the rhynchodaeum. *Aforia lepta* probably is an exception. The proboscis epithelium of this species is formed by very tall, thin, gobletlike cells (Figure 8B). It is difficult to imagine that such cells would remain undamaged during proboscis stretching and functioning in the environment. The relative small size of the proboscis, as compared to the proboscis sheath, seems also to be evidence that extension of this species' proboscis is limited only to the rhynchocoel. In all *Aforia* species, the proboscis retractor muscles are represented by several moderately thick muscle bands situated at the cavity perimeter along the proboscis lumen. The most powerful muscles are attached to the inner side of the body haemocoel wall. The retractors pass near the proboscis walls to join often with the inner (lon-

Table 2

Dependence of relative length of marginal teeth of *Aforia* radulae on depth of species habituation.

Groups of species	Depths of habituation of studied specimens (meters)	Shell height–tooth length ratio
A. circinata, A. kinkaidi	100–240	150–180
A. lepta, A. moskalevi, A. crebristriata	1200–3030	100–113
A. aulaca alaskana, A. kupriyanovi, A. abyssalis	3460–5220	57–90

gitudinal) muscle layer of the proboscis wall. The retractors are always connected both with the proboscis walls and the buccal tube by numerous muscle fibers.

The buccal tube leads from the buccal mass to the mouth at the proboscis tip. In all species, the buccal tube is very thin, semitransparent and is formed by one layer of epithelial cells surrounded by a layer of circular muscles of different thickness. The possibility cannot be excluded that the buccal tube is capable of peristaltic movements. In all *Aforia* species except *A. circinata* the buccal tube forms a fold (sometimes double) directed backward along the buccal mass walls. The functional significance of this fold remains unclear. In its anterior part the buccal tube forms an enlargement of various sizes surrounded by a sphincter used for holding a single marginal tooth. The anterior part of the proboscis is capable, at least in some species, of introverting during contractions of the proboscis retractors. This is most obvious in the morphology of the proboscis tip in *A. lepta* and *A. aulaca alaskana*. Retraction of the proboscis tip can be judged by the epithelium structure. The anterior part of the buccal tube in these species has the same kind of epithelium as the outer proboscis wall (Figures 8B, 12G). However, at some distance from the proboscis tip, the lining of the tube is as on the remainder of the buccal tube. We believe that this change in epithelial structure may be explained by introverting of the proboscis tip.

The size of the usually powerful buccal mass is variable in comparison with the proboscis length. The smallest relative size of the buccal mass is in *Aforia aulaca alaskana* and the largest is in *A. kupriyanovi*.

The boundary line between the back part of the buccal mass and the oesophagus can be usually determined by the place of an abrupt enlargement of the digestive tube diameter near the opening of the poison gland. At that region the thick layer of circular muscles that constitute the major part of buccal mass wall becomes much thinner.

The radula is situated at the bottom of the buccal cavity. The radular sac, containing the radula frontal part and the odontophore, is connected with the buccal cavity through

a relatively long and narrow duct. All species except *Aforia lepta* have more or less well developed odontophore cartilages. *Aforia circinata*, *A. abyssalis*, and *A. moskalevi* have four cartilages which lie symmetrically, two on each side of the odontophore. At the anterior part of the odontophore, the cartilages of each pair join and a thick, muscular symphysis connects the two newly formed cartilages. The radula bends over this symphysis. *Aforia crebristriata* has only two cartilages, which join in the anterior part of the odontophore. This species also has the largest cartilages (Figure 10B). *Aforia lepta* lacks the cartilage tissue but has a thick transverse muscle over which the radula bends. Relatively good development of the odontophore and the muscles connected with it seems to indicate that radular mobility is sufficient to allow the odontophore to protrude into the buccal cavity. The inner cavity of the anterior part of the radular sac is lined with a thick cuticular layer which prevents damage to the walls during radula movements.

The morphology of the radular marginal teeth was studied with the scanning electron microscope. Each tooth appears to consist of two parts or plates (Figures 3D, 4B–D) which are free at the base of the tooth and flow together at its tip. One of them has a thin ligament by which the tooth is connected with the radular membrane. Sections of the tooth show that in the proximal part both plates are also connected with a cuticular membrane (Figure 4C). The upper plate of the tooth is more rounded and the lower one is crescent-shaped. These plates and the membrane are differently stained by Mallory: the formers are bright orange and the latter is dark blue. The plates and membrane form a groove along both sides of the tooth. The relative length of the marginal tooth (the shell height–tooth length ratio) varies markedly among species, from 57 (*A. kupriyanovi*) to 180 (*A. circinata*). By comparing this ratio with the bathymetric distribution of the species, one can see that tooth length increases with the transition from sublittoral to bathyal and to upper and lower abyssal species (Table 2).

The poison gland is long, well developed, and powerful in all species; it forms tight convolutions. The gland opens approximately at the border between the buccal mass and the oesophagus and rather distant from the opening of the radular sac into the buccal cavity. This may indicate that all of the inner cavity of the proboscis is filled with poisonous liquid. The size of the muscular bulb varies: *Aforia lepta* has the smallest one, *A. abyssalis* has the largest one, and the muscular bulbs of *A. crebristriata* and *A. moskalevi* are of medium size. All species have a rather small lumen in the bulb, usually adjacent to the opening of the poison gland. The walls of the muscular bulb are formed by two layers of muscles, longitudinal and circular, which are not separated by an intermediate layer of connective tissue as in Conidae (HYMAN, 1967).

All *Aforia* species have large salivary glands situated under the nerve ring. In *A. circinata*, *A. moskalevi*, and *A. crebristriata*, the glands are united into a single mass. The salivary ducts are always paired and weakly coiled.

They open into a duct connecting the radular sac with the buccal cavity. Proximal parts of the salivary ducts run within the wall of the buccal cavity. Most parts of the ducts are lined with a ciliary epithelium, which provides transport for the gland secretion. As the duct opening is approached, the ciliary epithelium is replaced by a smooth one.

All *Aforia* species have differently developed rhynchostomal lips, which are rounded muscular folds forming a kind of funnel at the anterior side of the head. The rhynchostome has a large powerful sphincter obviously used in catching prey.

Other systems of organs of studied *Aforia* species are the same as in other families of neogastropods. Morphology of the mantle complex is similar in all species and is characterized by substantial development of the gill and the osphradium. The large sizes of the mentioned organs may be conditioned by a low density of food resources at great depths and by the necessity of an active mode of life. This requires (1) high oxygen consumption, which is provided by a large gill, and (2) the necessity of well-developed chemoreception, which demands a considerable development of the osphradium (KANTOR & SYSOEV, 1986).

Functional Analysis of Morphology
of the Digestive System

Recently, many authors have paid attention to morphofunctional specializations of the digestive system of Turridae (SMITH, 1967; SHIMEK, 1975; SHERIDAN et al., 1973; SHIMEK & KOHN, 1981). Most important is the examination of the anterior part of the digestive system and radula, which are the most variable among turrids. Morphological and functional types of turrid radulae were analyzed by SHIMEK & KOHN (1981). According to the classification proposed by those authors, *Aforia,* like other representatives of the subfamily Turriculinae, has a slicing radula used for tearing the prey body. The radulae of all other Turridae, with well-developed subradular membranes and mainly with "nontoxoglossate" solid marginal teeth, are classified as slicing, slicing-rasping, and slicing-stabbing types of radulae.

However, the functional types of "nontoxoglossate" radulae and the correspondent mechanisms of functioning proposed by Shimek & Kohn cannot explain many facts. The buccal mass with radula is situated at the base of the proboscis in all Toxoglossa and cannot be moved out through the mouth as in other prosobranchiate gastropods. Therefore, slicing the prey as supposed by Shimek & Kohn can take place only in the buccal cavity after the prey is already caught and partially swallowed. In this connection, the presence of a well-developed, large poison gland in "nontoxoglossan" Turridae cannot be explained, because envenomation of the prey inside the buccal cavity would seem useless. On the other hand, the poison gland disappears during reduction of the radula, and prey capture by species with a reduced radula occurs with the help of proboscis

or enlarged rhynchostomal lips (KANTOR & SYSOEV, 1986). Using the classification of SHIMEK & KOHN (1981) it is impossible to explain the functioning of such a specialized radula as in *Imaclava unimaculata* (subfamily Clavinae) which has true "toxoglossate" hollow marginal teeth along with a central one and well-developed laterals. It is difficult to imagine the mechanism by which poison would be passed through the hollow marginal tooth or its usefulness, as soon the buccal cavity would be filled with the poisonous liquid. MAES (1983) has also put forward reasonable doubts about the slicing function of Clavinae radulae. She considered that the radula of *Drillia cydia* is used not for tearing but for holding and perforating the prey, a fact confirmed by finding almost intact polychaetes in the mollusk's stomach.

Thus, the hypothesis of a "slicing" or "slicing-stabbing" function of turrid radulae possessing a well-developed subradular membrane is not in agreement with many data.

In this connection, the findings of single marginal teeth held by a sphincter of the proboscis tip in three *Aforia* species (*A. moskalevi, A. kupriyanovi,* and *A. abyssalis*) is of great interest. Morphology of the distal part of the proboscis of other species also confirms the possibility that the marginal tooth is held by the sphincter. The only possible explanation of the fact is that marginal teeth, removed from the subradular membrane in the sublingual pouch during radular degeneration, are used at the proboscis tip for stabbing prey and poisoning them with poisonous liquid in a fashion similar (but not identical) to that used in higher Toxoglossa. Grooves running along both sides of the tooth (see above) could be used for administering the poison. Thus, the radula of *Aforia* species has two functions. The first is to stab the prey with the single marginal tooth at the proboscis tip and to use the radula as a whole in the buccal cavity. The second function is to a great extent unclear for *Aforia.* It is possible that the radula, which can move out to some extent into the buccal cavity, is used to move the prey from the buccal cavity to the oesophagus and probably for damaging the prey tissues. In particular, this second function is confirmed by the structure of the central tooth, which has one rather large cusp on the frontal edge.

One can suppose that using the marginal teeth at the proboscis tip is almost universal among turrids with a well-developed subradular membrane. The fact is confirmed by our finding of a marginal tooth at the tip of the proboscis of *Splendrillia* sp. (subfamily Clavinae). The function of the hollow marginal tooth of *Imaclava unimaculata* also becomes obvious: the mollusk uses it at the proboscis tip as higher Toxoglossa do.

Evolution of the radular apparatus is closely associated with the evolution and morphology of the proboscis. SMITH (1967) described a new type of proboscis of prosobranch gastropods, an intraembolic one characterized by circular folds formed by proboscis walls in their contracted state. When describing the buccal apparatus of *Oenopota levidensis,* SHIMEK (1975) advanced the notion of the intraem-

bolic proboscis and postulated that its principal feature was the existence of a permanent rhynchodaeum; this means that not the whole rhynchodaeum of the intraembolic proboscis participates in the proboscis everting. However, in many gastropods with a pleurembolic proboscis, even when the proboscis is completley everted a part of the rhynchodaeum remains inside. A special subtype of pleurembolic proboscis, the extraembolic type, was proposed for gastropods in which the whole rhynchodaeum takes part in the proboscis eversion and the proboscis sheath is absent during the complete eversion of the proboscis (KANTOR, 1985).

Investigation of the proboscis morphology of several species of *Aforia* allows us to state that all species of the genus lack an invaginable part of the rhynchodaeum; that is, everting of the proboscis results only from its stretching. Comparison of *Aforia* with other turrids leads to a conclusion that the main characteristics of the intraembolic proboscis are the absence of the invaginable part of the rhynchodaeum and the localization of the buccal mass at the proboscis base.

Differences in the displacement of the buccal mass are the most important differences between the intraembolic and pleurembolic probosces as well as between rachiglossan and toxoglossan neogastropods in general. In fact, during the origination of the proboscis by elongation of the ancestral form snout, the elongation of the anterior oesophagus in front of the nerve ring occurred in rachiglossan families while elongation of the buccal tube connecting the buccal cavity with the mouth occurred in toxoglossan groups (PONDER, 1973). Thus, the two proboscis types have different origins and are not homologous. Formation of concentric telescopic folds within the walls of the intraembolic proboscis serve to enhance its elongation.

The origin of the intraembolic type of proboscis may be connected with the origin and development of the poison gland. This process may be presented in the following way: the poison gland that appeared in the toxoglossan ancestor at the first stages of evolution was closely associated with the radular apparatus. Probably the efficiency of the poison gland and the poison itself was much lower than in modern species. This required maximal proximity of the administered poison to the radula that was damaging the prey tissue. At the same time elongation of the proboscis and the appearance of the poison gland allowed "distant feeding" on actively moving prey. Elongation of the proboscis appears to be closely related to poison gland enlargement; as the inner volume of the proboscis grew, more poison was needed to fill it. Formation of a powerful poison gland, which already did not fit the proboscis, prevented the gland from everting together with the proboscis. At the same time, distancing the radular apparatus from the opening of the poison gland hampered the use of the poison. This caused, in turn, fixation of the buccal mass at the proboscis base. Most probably during that period of evolution the mechanism developed of using marginal teeth at the proboscis tip for stabbing the prey. Using the marginal teeth at the proboscis tip did not require any considerable morphological changes of the anterior part of the digestive apparatus: in all prosobranch gastropods, the subradular membrane degenerates in the sublingual pouch and worn teeth are removed via the digestive tract. By contrast in toxoglossan gastropods, teeth that separate from the subradular membrane are transferred to the proboscis tip where they were held by the sphincter. Using the single tooth at the proboscis tip allowed a considerable elongation of the proboscis because the function of stabbing the prey was no longer associated with the radular apparatus per se. Therefore, the appearance of the intraembolic proboscis is associated with the appearance of the poison gland, transition to "distant feeding" on actively moving animals, and using the marginal tooth at the proboscis tip.

If the proposed scheme of evolution of the anterior digestive apparatus is adopted, one can easily understand also the appearance of the typically "toxoglossan" mode of feeding as in higher Turridae and Conidae which possess only hollow marginal teeth acting as a syringe needle. As the proboscis elongated, the main radular function became stabbing the prey with the individual tooth at the proboscis tip. This led to reduction of the odontophore and, consequently, of the subradular membrane. Thus, *Aforia* is a kind of intermediate morphological stage transitional to the typical "toxoglossate" forms. However, *Aforia* cannot be considered as an intermediate evolutionary stage because modern turrids with a well-developed subradular membrane often are more numerous than the typical toxoglossan forms; "nontoxoglossate" turrids should be considered as a result of evolution of a separate evolutionary line (or lines), which is not the same as that resulting in "true toxoglossates." Probably, use of the radula not only at the proboscis tip but also in the buccal cavity has some advantages. If the radula were not used in the buccal cavity it would be difficult to explain the existence of numerous species of the subfamily Clavinae having, besides marginal teeth, also central and large, powerful lateral teeth.

The mechanism of transporting the tooth from the radular sac to the proboscis tip in *Aforia* is presently unclear. Pushing the tooth, separated from the membrane, into the buccal cavity occurs probably by the contraction of the powerful circular musculature of the radular sac. Transportation of the tooth to the proboscis tip may occur along with the flow of poisonous liquid during contraction of the muscular bulb or also by peristaltic movements of circular muscle fibers of the buccal tube. The position of the proboscis sphincter and the length of the marginal tooth are correlated so that the tooth, held at its base by the sphincter, extends outside the proboscis. In this connection it is interesting to analyze the morphology of the proboscis tip of *A. aulaca alaskana* (Figure 12G). If one supposes that the well-developed sphincter of the buccal tube is intended to fix the tooth base, then the point of the tooth would not protrude outside the proboscis. As has been mentioned above, in this species, the proboscis tip can be everted and after eversion the tooth point appears to be protruded outside. One can propose that such a mechanism was developed to protect the rhynchodaeum during eversion of the proboscis with the already held tooth and also to protect

the tooth itself, as searching for prey is probably carried out by a sense of touch of the proboscis tip. Transportation of the tooth from the radular sac to the proboscis tip most probably occurs at the moment of drawing the proboscis into the rhynchodaeum because in this case the distance from the buccal mass to the proboscis tip is much less than that in the everted proboscis.

History of the *Aforia* Fauna

The genus under consideration is closest to the genera *Leucosyrinx* Dall, 1889, *Comitas* Finlay, 1926, *Parasyrinx* Finlay, 1924, and *Turrinosyrinx* Hickman, 1976. These genera are apparently interrelated and have a common ancestor.

The earliest certain findings of fossil species of *Aforia* are known from the Oligocene. From the upper Oligocene of northwestern North America, a rather diverse fauna of *Aforia,* consisting of four species, has been recorded (JA-VIDPOUR, 1973). At present, a single finding of a Paleogene species is known from the northwestern Pacific. The species related to *A. clallamensis* (Weaver, 1916) was found, according to unpublished data of V. N. Sinelnikova and A. E. Oleynik, in deposits of western Kamchatka (Rategin suite). However, dating of this suite currently is rather uncertain (upper Eocene or upper Oligocene—A. E. Oleynik, personal communication).

Apparently the geographical center of the species diversity is the northern Pacific, with the most intensive formation of species being in its northeastern region. This is evident both from the relatively high diversity of fossil *Aforia* species in this region and from the fact that the highest morphological diversity of recent species is from the Pacific coast of North America, the only region where representatives of all the subgenera live.

Recent species of *Aforia* demonstrate an association with low water temperatures, living generally in bathyal and abyssal zones and rising into shallow waters only in high boreal and Antarctic regions. One can confidently consider that life in cold waters was characteristic of this genus during all of its history and that adaptation to cold water has conditioned the formative history of the recent fauna of the genus.

The first Cenozoic phase of colder climates in the northern Pacific began in the second part of the Eocene (KA-FANOV, 1982). Precisely in this period, formation of the genus began. The temperature minimum was most pronounced in the middle Oligocene (KAFANOV, 1982), and, after achieving it, various and numerous upper Oligocene *Aforia* fauna developed. However, some warming of the climate in the northeastern Pacific began later in the Oligocene (WOLFE & HOPKINS, 1967), reaching its maximum in the northern Pacific at the end of the early or beginning of the middle Miocene (KAFANOV, 1982). These facts are well correlated with the disappearance of most of *Afloria* species at the border between the Oligocene and Miocene in fossil formations of the northwestern part of the U.S.A., with the single species being recorded at the very early

Miocene (JAVIDPOUR, 1973). Apparently this disappearance was related to the leaving of *Aforia* species for bathyal and abyssal regions of the northern Pacific. Representatives of the deep-sea Miocene fauna are not known, but a reason exists that forces us to consider that there was a rather well-developed deep-sea fauna of *Aforia* in the Miocene. At present there are two closely related species living in the abyssal regions of the northern Pacific and northern Atlantic respectively—*A. abyssalis* and *A. hypomela*. Obviously these two species are relicts of the early Miocene deep-sea fauna of Central America. Geographical separation of the species resulted from the forming of the central American isthmus and the closing of the deep-sea connection between the Pacific and the Atlantic, which are dated to the middle Miocene (for a review of this subject see NESIS, 1985).

One can suppose that, precisely in the Miocene, migrations of bathyal species began southward along the Pacific coast of North and South America. Similar migrations have been reconstructed in the geological history of many other groups of animals (NESIS, 1985). Presently, the movement of *Aforia* representatives southward is traced by the distribution of recent bathyal and abyssal species and subspecies from the eastern Pacific (POWELL, 1951; present data).

The late Miocene Nuvok transgression (KAFANOV, 1982) has led to the forming of a connection between the north Pacific and Polar basins, which in turn caused a cooling of the climate. In this respect, a gradual rising of *Aforia* species to more shallow zones, including the western Pacific, began during the Pliocene. An earlier Pliocene finding of *Aforia* is recorded from the Tomya Formation of Honshu (OTUKA, 1949) which is characterized by a relatively deep-sea (bathyal) fauna (OKUTANI, 1968). Also at the Pliocene *A. circinata* appears on the shelf of the Gulf of Alaska (JAVIDPOUR, 1973) and in deposits of eastern Kamchatka (PETROV, 1982). Thus, just at the Pliocene, the fauna of *Aforia* obtained its principal features of its Recent appearance and distribution.

The rising of a part of the species to shallow but cold zones took place also in the southern Pacific. Some Antarctic species that migrated from the northern Pacific along the American coast have settled in the shallow zone for a second time, rising up to the sublittoral. The rising of *Aforia* species to shallow waters in Antarctic regions, while species distributed in tropical and subtropical latitudes retained their relation within deep-sea habits, has been analyzed in detail by POWELL (1951).

Presently the main part of *Aforia* species live in the Pacific, being distributed almost circumoceanically except for the western Pacific (Rukue Islands at the north to Macquarie Island at the south). A single species (*A. hypomela*) is recorded from the northern Atlantic and two species (*A. gonioides* and *A. magnifica*) penetrate into the southwestern Atlantic. Another two species penetrate also into the southern part of the Indian Ocean (*A. lepta* and *A. staminea*). Most species show a near-continental distribution.

ACKNOWLEDGMENTS

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